

Territorial behaviour associated with feeding in both sexes of the tropical zygopteran, *Libellago hyalina* (Odonata: Chlorocyphidae)

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ABSTRACT

Territorial behaviour associated with adult odonate feeding in a Bornean rain forest under-storey is described and its underlying causes are analysed. Immature males and females of all ages of *Libellago hyalina* defended perches along a narrow trail in kerangas forest, concentrating especially around patches of sunlight. Throughout the day there was displacement of individuals as the illuminated areas moved and population levels of foragers increased, with maximal density from 13:00 - 15:00 h, but territorial success which followed physical combat could not be associated with size, sex or age. Foraging rates were also highest in this period but peaked clearly at 14:00 h. Both foraging attack rates and attack success were higher in sun patches than in shaded territories. Potential prey, mostly small Diptera < 4 mm length, were more abundant along the trail than in the surrounding forest, but were not concentrated in sunlight. It is suggested that, against the dark backdrop of the forest under-storey, prey became much more visible in sunlight, and were more easily detected and more easily captured, hence sites near sun patches were strongly contested. This behaviour constitutes a hitherto undescribed foraging strategy, which may be characterized as follows: "increasing capture success by concentrating in situations where prey visibility is enhanced by overhead sunlight against a dark background." It is suggested this strategy may be common in tropical rain forest, home to a majority of Odonata species.

INTRODUCTION

Within the tropical rain forest under-storey it is common to encounter odonates perched on vegetation far from water. Typically, this behaviour is observed along forest trails and in Borneo has been reported in species such as *Tyriobapta torrida* Kirby (Libellulidae), which perches on tree trunks in large numbers, or *Vestalis amabilis* Lieftinck (Calopterygidae) (Thompson 2000) and *Libellago hyalina* (Selys) (Chlorocyphidae), which both perch on bare twigs and leaves (Orr 2001).

Both males and females may be present, often with the latter predominating. Immatures may also be disproportionately represented. The behaviour apparently occurs in closed canopy forest in all parts of the world's tropics.

It is generally believed that the odonates establish feeding territories, possibly in areas of high prey density, or in situations where prey can be more easily captured. The evidence supporting this interpretation comes mostly from direct observation (e.g. Orr 2001) and is supported by the following. In most known cases both males and females station themselves around gaps or on fringing vegetation along man-made trails, more or less evenly spaced so far as perch distribution allows. Both males and females interact aggressively with members of their own sex and with members of the opposite sex, buffeting and chasing each other, sometimes colliding in a clash of wings. Sometimes contests occur between members of different species but the bulk of aggressive interactions are between conspecifics. Generally, regular feeding is observed with frequent forays away from perches to take prey. It is often after such a flight that a territorial dispute will ensue. Feeding territories have also been recognized in some temperate species (e.g. Parr 1983; Baird & May 1987; Gorb 1994), lending weight to this interpretation.

The subject has received limited attention, mainly because little quantitative behavioural research has been conducted in tropical rain forest where the behaviour is most often observed. It is however in this habitat that the majority of Odonata species live, hence this foraging strategy may form a very significant part of the behavioural repertoire of the order. Here I present the results of an investigation into the territorial behaviour of males and females of the small Sondaic chlorocyphid *Libellago hyalina* along a forest path far from the breeding site. I examine some of the factors involved in determining territory preferences and their possible biological bases.

Table 1. Taxonomic breakdown of Malaise trap samples based on total numbers of individuals.

Order	Number	Percent of total
Diptera	1,067	77.8
Hymenoptera	162	11.8
Coleoptera	45	3.8
Hemiptera	33	2.4
Orthoptera	32	2.3
Lepidoptera	17	1.2
Psocoptera	8	< 1
Isoptera	6	< 1
Strepsiptera	1	< 1
Total	1,371	100

AREA AND METHODS

The study took place in Badas Forest Reserve (4°34'N, 114°25'E; 40 m a.s.l.), Brunei along a 30 m section of a narrow vehicular track running almost exactly east-west; the approximate locality is illustrated in Orr (2003: 19, fig. 11). The vegetation was tropical heath forest (known locally as kerangas), growing on a sandy substrate, characterized by microphyll sclerophyllous vegetation dominated by the conifer *Agathis borneensis*. Under-storey growth was dense. Other common odonates in the immediate area included the libellulids *Brachygonia oculata* (Brauer) and *Agrionoptera sexlineata* Selys. The nearest breeding habitat was a natural black-water drain some 300 m distant flowing through alluvial swamp forest and into the Belait river about 800 m distant. *Libellago hyalina* was observed every day from 08:00 - 17:00 h from 18-23 March 1996. The weather was sunny throughout most of this period, which included the equinox, and local time was very close to solar time. Shade temperatures ranged from 28-32°C throughout the day. As the sun was almost directly overhead, and given the orientation of the track, the daily arc of the sun lay almost in the same plane as the study transect, resulting in a fairly regular shifting pattern of sun patches throughout the day. The area was mapped roughly with reference to a length of raffia, graduated at 2 m intervals, laid along the length of the transect. Bordering vegetation between 1-2 m height was recorded along with the areas of sun patches at different times of the day (09:00 h, 12:00 h and 15:00 h).

When first encountered in the study area individuals were captured, measured and marked. The hindwing length was measured with vernier callipers. Using superfine waterproof felt pens (Faber-Castell™), individuals were marked on the left forewing with a unique linear array of one, two or three spots using different permutations of red, green and black. It was thus possible to recognize up to 39 individuals of each sex without further capture (in a few cases a fourth mark was added as necessary). Individuals were designated F1 – Fn for females in order of capture and M1 – Mn for males. The position of each individual present in the transect, including its height above the ground, was recorded hourly each day from 09:00 - 15:00 h. It was noted whether the individual perched in direct sunlight, or at least in partial shade. This general census required about 10 min. Dispersion was assessed by analysis of nearest-neighbour distances (Clark & Evans 1954), in a total area about twice the path width. This area was chosen because the assumptions of the model are approximated. A greater area would measure a spurious contagion, as odonates clustered around the favoured habitat, and a smaller area, with perches around the boundary, would measure spurious avoidance.

Every hour, between general censuses, territorial interactions and feeding behaviour were observed and recorded from two stations, one in a sunlit area and one in a shaded area. About 20 min was spent at each station observing 1-5 individuals. Both the rate of feeding flights and the success of each attack were recorded as far as was possible, the latter judged after foraging flights by inspecting the odonates on their perches for signs of prey in their mouths or obvious chewing motions. Visual observations on prey density were also noted. Throughout the results, unless otherwise stated, error was estimated using standard deviations.

In order to obtain information on possible prey available and its distribution within the forest four standard Malaise traps (trapping head 1.9 m wide x 1.3 m high) of fine black netting were set in the area. Two were set on the track, outside the study area separated from each other by a distance of 50 m. One was oriented parallel to the track and one at right angles to it. Two other traps were set inside the forest 30-40 m distant from the track at the same orientations as the first two, orthogonal to each other. In order to exclude nocturnal insects the traps were closed each evening ca 17:30 h and opened each morning. The collecting bottles, each containing 70% ethanol, were left in place for five days after which the total catch was sorted, with each specimen identified to order and its body length measured.

RESULTS

Distribution of sun patches

The distribution of light was irregular, with dappled areas interspersed with patches of strong sunlight and deep shade, a consequence of the complex multilayered canopy above. The location of sun patches shifted constantly throughout the day. Patches tended to shift from west to east as expected from the relative motion of the sun and tended to be more concentrated at midday and more attenuated and broken in the morning and afternoon (Fig. 1). Sun patches accounted for ca 30% of the transect at 12:00 h but 50% at 15:00 h.

General population statistics

Over the five day period, a total of 68 individuals of *Libellago hyalina* was marked, 44 females and 24 males. Of these 35 females were clearly immature, 9 were mature. All males were immature. The average maximum number of individuals per day along the transect at a given time was 19.6 (range 15-27). There was an average return rate of 59% of individuals from the previous day. The mean hindwing length of males was 17.52 mm ($s = 0.43$), of females 18.41 mm ($s = 0.67$).

Distribution of perches in space and time

L. hyalina arrived in the area first around 09:00 h, steadily increasing their numbers until about 13:00 h when numbers peaked and remained fairly constant until about 15:30 h. After this time numbers diminished and none was seen after 17:00 h (Fig. 2). As evident from Figure 1 the first individuals to arrive perched preferentially near sun patches and perches near shaded areas were occupied later. However most individuals perched out of direct sunlight. Around sun patches 72% of individuals were recorded on at least partially shaded perches, even when apparently good perches were vacant in direct sunlight; around shaded areas 96% of individuals perched in shade, even when potential perches in small sun flecks were available.

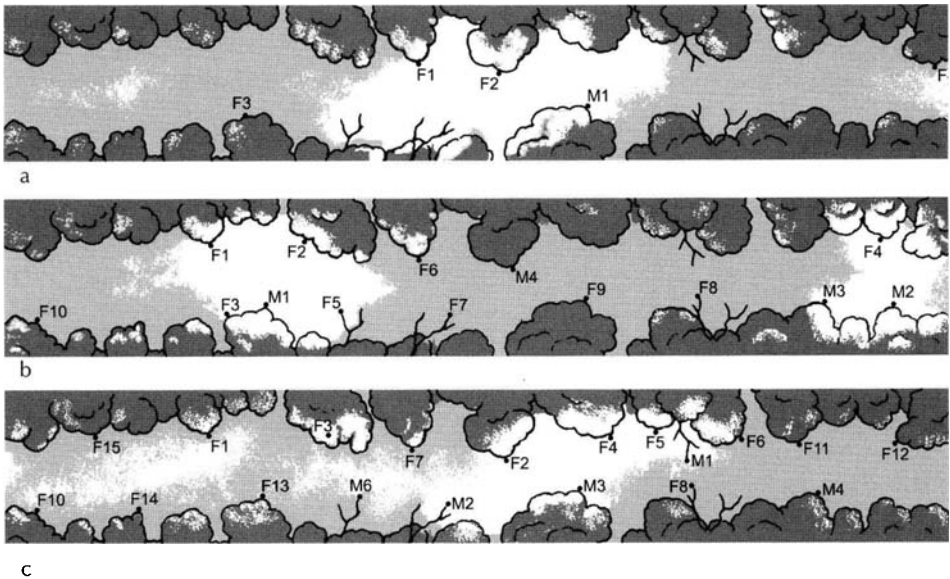


Figure 1: Plan of the study area on the first day of observations. Positions of sunspots and territorial perching females (F1-F15) and males (M1-M5) of *Libellago hyalina* are shown at (a) 09:00 h; (b) 12:00 h; and (c) 15:00 h. Transect length 30 m.

Almost all perched between 1-2 m above the ground on either leaves or bare twigs, facing toward the open space of the track. Analysis of nearest-neighbour distances for each day, including all values recorded from 12:00 - 17:00 h, indicated that the overall distribution of individuals within the study area tended towards uniform at higher densities ($z = 3.2$ to $z = 5.5$; $p < 0.001$), suggesting a mechanism of mutual avoidance. At times of high density, overall density around sun patches was significantly higher than in shaded areas. This was shown by analysis of nearest-neighbour distances of individuals around sun patches and those in deep shade at 12:00 h, the time when the sun patches were best defined ($\bar{x}_{\text{sun}} = 1.99 \pm 0.39$ m, $\bar{x}_{\text{shade}} = 3.10 \pm 0.92$ m, $t_{70} = 3.45$, $p < 0.001$). No significant differences in size (hindwing length) were detected between individuals around sun patches and those in shade. Nor was there any evidence that either maturity or sex influenced distribution relative to sun patches and shade.

Individuals did not remain on the same perch all day, but instead followed the shifting sun patches (Fig. 1). Inevitably this led to small scale rearrangements of individuals relative to each other. Even though the set of individuals occupying sunlit perches or perches on the edge of sunlight remained remarkably constant each day, and typically included those individuals earliest to arrive. At the time of maximal density, which each day fell between 13:00 h and 15:00 h, 82% of individuals which had arrived before 11:00 h ($n = 56$) were stationed near sunlight, whereas only 53% of those arriving after 11:30 h ($n = 47$) were near sun. When individuals occupying sunny positions at 12:00 h ($n = 59$) were traced until 15:00 h, it was

found that 86% remained near sun patches. Conversely 62% of those in deep shadow at 12:00 h ($n = 37$) remained there at 15:00 h, with many of the other 38% passively moving nearer to sunlight later in the day as the sun patches became more diffuse and extensive. The situation, however, was dynamic, with insects perched in shade passively coming to occupy sunlit positions as the sun patches moved. At the same time individuals originally near a sun patch, which were left behind in shadow, frequently remained on their original perch for 5-15 min before seeking a new position in the sun. It was in these situations that the most vigorous territorial contests occurred. Overall, ca 15% of individuals recorded through the day had disappeared from the transect by 15:00 h, probably dispersing to nearby areas along the track.

From one day to the next the situation was less clear, owing to the relatively high turnover mentioned above. However three individuals (F4, F6 and F8) returned to the site for five consecutive days and almost always occupied positions around sun patches. No individual remaining predominantly in shadow was recorded for more than two consecutive days.

Territorial interactions

In some respects interactions were similar to agonistic behaviour observed between mature males at breeding territories. Actions included perching nearby (10-20 cm distant), hovering face to face for 1-2 s, high-speed chases and physically buffeting perched or airborne antagonists. These actions were not as frequent or as intense as in territorial males at breeding sites.

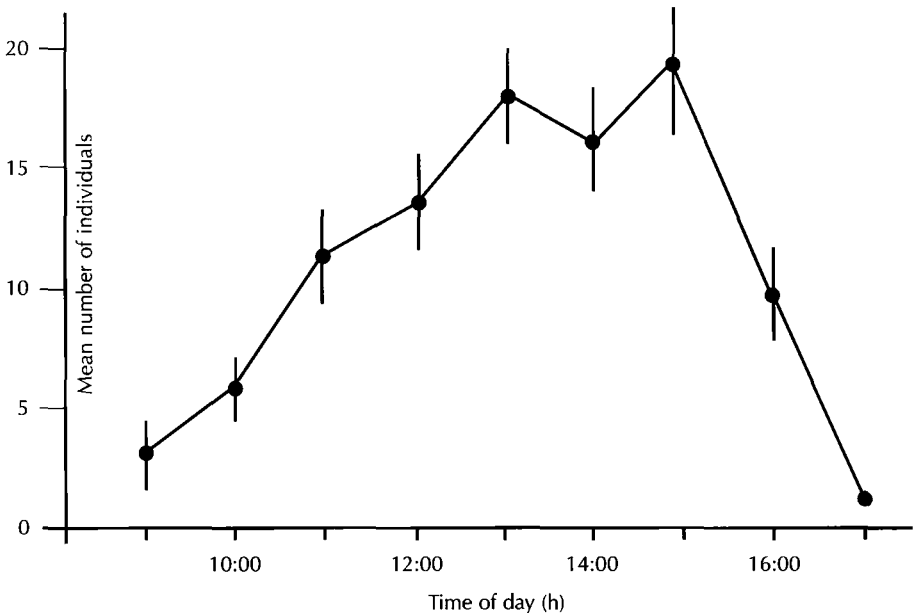


Figure 2: Mean total number of *Libellago hyalina* individuals (± 1 s.d.) perched in the study area from 09:00 h to 17:00 h.

In total, 87 interactions were observed. These could be classified as follows (including non-occurring possible combinations):

- (1) Newly arriving individual at sunspot contesting with resident (19 cases)
- (2) Newly arriving individual in shade contesting with resident (7 cases)
- (3) An individual from a sunspot recently shaded relocating to an occupied territory which had recently been exposed to the sun (21 cases).
- (4) The reverse of 3, an individual cast into sunlight relocating to contest territory in shade (0 cases). This did not count displaced individuals contesting territory in shade, which are treated as 8.
- (5) An individual originally in shade attempting to relocate to sun (5 cases)
- (6) An individual originally in sun attempting to relocate to shade (0 cases)
- (7) Encounters between neighbours in sun (26 cases)
- (8) Encounters between neighbours in shade (9 cases)

Of the sample of 87 observed contests, many more occurred near sunny stations than in shade (71:16 respectively). Moreover, there was a definite trend to move from perches in shaded locations to those around sun patches. Ignoring new arrivals and contests between neighbours in either sun or shade leaves 26 encounters in which an individual from a shaded perch challenged the occupant of a perch near the sun, whereas there were no encounters where individuals attempted a voluntary move from near the sun to the shade. The significance of this value is obvious.

Examining the number of aggressive interactions between females, between males and between males and females, there was a greater level of activity involving females than expected by chance, given the observed sex ratio. However this difference was not significant ($\chi^2 = 5.31$, $df = 3$), meaning the present observations are consistent with a model of random interactions within and between sexes. No significant advantage accruing to larger individuals was detected in any type of territorial interaction, but it must be noted that the sample sizes are quite small in relation to the relatively small variation in size in both sexes.

Feeding patterns

Feeding activity [general pattern]

A total of 356 feeding attacks was recorded. Individuals waited on their perches and made frequent sorties, horizontal or shallow flights of 0.5-1.5 m into open space from where they returned immediately to their perch. The duration of these feeding flights lasted from 1-5 s and did not normally involve an encounter with another individual. Activity was measured by sorties per individual per hour (extrapolated from a 15-20 min observation period). The general pattern of feeding activity is shown by Figure 3. Beginning around 09:00 h, the rate of feeding peaked initially about 11:00 h, dipped at 12:00 h, then increased sharply from 13:00 h to a maximum at 14:00 h and remained high until about 15:30 h. From day to day and from individual to individual the recorded rates of feeding for a particular time period were quite variable as indicated by the error bars (standard deviations) in Figure 3.

When an individual returned to its perch, it was inspected for presence or absence of prey in its mouth, frequently revealed by chewing motions of the jaws. The mean head width of *L. hyalina* (including the eyes) was near 4 mm, a measurement which facilitated the estimation of prey size. Overall, 72% of all strikes observed resulted in visible prey. However, 21% of observed strikes were discarded from further analysis as observation of presence or absence of prey was inconclusive. Of the remaining sample ($n = 281$), 91% of strikes were successful. In the remaining 9% of cases, it is believed no prey was captured. It was seldom possible to identify prey items with certainty, but all observed were estimated to lie in the size range 1-2.5 mm in length and it is probable that small Diptera formed the bulk of the diet.

Differences in feeding intensity and efficiency in shade and sun

The mean strike rate (MSR) measured in sorties per individual per hour (SPIPH) was 10.37 ± 9.32 SPIPH. For sunlit patches $MSR_{\text{sun}} = 14.53 \pm 8.75$ SPIPH and for shaded patches $MSR_{\text{shade}} = 6.35 \pm 4.34$ SPIPH.

Progressive changes in feeding activity throughout the day resulted in high standard deviations in the MSR. However, based on 40 paired comparisons of mean values for each observation period for each day (the 17:00 h data were omitted) the attack rates by individuals in sun patches were significantly higher than those of individuals in shaded areas (Sign test, $T = 33$, $p < 0.001$).

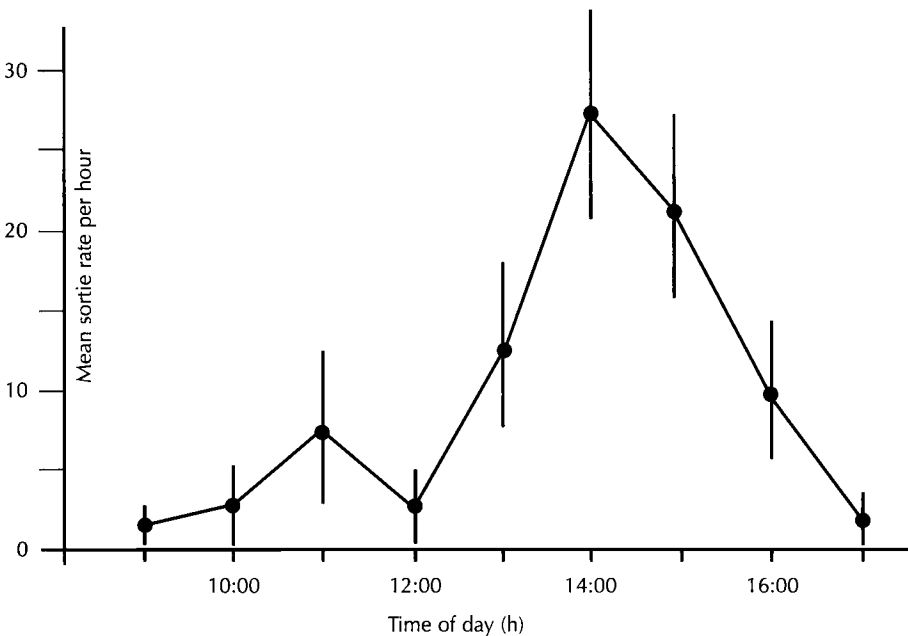


Figure 3: Mean foraging rates (± 1 s.d.) in *Libellago hyalina* from 09:00 h to 17:00 h in the study area.

Individuals foraging in sunlight scored a 95% success rate in securing a prey item on a foraging flight ($n = 182$). Those foraging in shade scored only an 83% success rate ($n = 99$). If the converse is considered, the rate of failure, it was evident that those in the shade consistently failed more often to secure prey (Test of proportions, $z = 3.82$, $p < 0.001$), suggesting that prey are captured more efficiently in sun patches.

Prey behaviour and patterns of density

It was not possible to measure prey density accurately, as the insects were too sparse to permit random spot samples with a net and, being very small, were impossible to assess visually. However, it is probable that the majority of potential prey were small Diptera using the open transect as a flight path. The activity appeared to increase in the afternoon (13:00 - 15:00 h), but mating swarms rarely formed. Of six swarms observed one was in sunlight and five were in shadow, and the former in particular provoked a feeding frenzy among the *L. hyalina*. It was not possible to record many feeding flights in detail.

Evidence of potential prey available, and their distribution and movement, was provided by the Malaise trap samples. A total of 1,371 insects was trapped, the taxonomic breakdown of which is given in Table 1. Diptera were by far the most abundant order, with small Nematocera, especially Ceratopogonidae, Culicidae and Chironomidae, particularly well represented.

Further analysis includes only insects up to 4 mm body length (that is, 98% of the sample), as prey items above this size were considered too large for *L. hyalina* to capture and kill. The total catches of insects in this size class is shown for the four traps grouped by orientation and position (Table 2).

There were substantial differences in the gross yields of the different traps ($\chi^2 = 149.6$, $df = 1$, $p < 0.001$). Moreover there were significantly more insects trapped on the track than in the forest ($\chi^2 = 39.6$, $df = 1$, $p < 0.001$) and on the track more than three times the number was taken by the trap mounted across the path than by the trap mounted length-wise along it ($\chi^2 = 129.7$, $df = 1$, $p < 0.001$). There was no difference between the yields of two orthogonally mounted traps in the forest ($\chi^2 = 4.03$, $df = 1$, n.s.). This suggests that even small insects preferentially use the opening as a flight path and fly along the track much more than across it. However in the unbroken under-storey, flight direction appears to be more random.

DISCUSSION

The results clearly show that *Libellago hyalina* individuals of both sexes defend small territories associated with feeding along forest paths. Prey density, inferred from direct observation and recorded feeding rates, is probably sufficiently low to promote competition for food, providing a basis for competition for favourable feeding perches. It is evident that perches in or near sun patches are preferred over perches in shade. Many of the components of male-male contests at breeding territories occur (Orr 1996), but interactions between feeding individuals are

generally of briefer duration and less intense. Contests never escalated into protracted parallel flights, described for this species by Orr (1996), in which mature males appear to display to each other and to females in bright sunlight.

As the occupancy of preferred sites is normally associated with success in combat, it is of interest to understand the causative factors involved. The obvious factor, size, with larger individuals occupying preferred territories, was not demonstrated. This failure may result from the small variation in size in the population and relatively small sample sizes, or it may reflect the interaction of other effects, such as hunger levels and general vigour, which cannot be measured independently. Moreover, although males were significantly smaller than females, there was no evidence that they were less competitive. This highlights the fact that males and females cannot necessarily be compared by the same criteria, as many asymmetries come into play.

A significant feature of the population was a fairly high turnover of individuals from day to day. This contrasts with the behaviour of males at breeding territories to which the same individuals return for many days running (Orr & Cranston 1996). Presumably observed turnover resulted from a combination of natural attrition, dispersal to other feeding sites and to breeding sites. Males were fewer in number than females, owing partly to a higher daily turnover. Only immature males were present, whereas 20% of all females were mature. Mature females may visit the area on alternate days, presumably ovipositing on other days. Such a pattern of oviposition has been observed in other studies on the species (A.G. Orr unpubl.). It seems reasonable to suppose that time spent at the feeding site is primarily a pre-reproductive 'fueling-up' by immatures or replenishment of protein by females exhausted by oogenesis. Mature males presumably spend most of their time at the water, feeding opportunistically near their breeding territories.

The present study demonstrates concentrated feeding behaviour along a forest trail. The results of Malaise trapping suggests that it is here that prey is also most concentrated. Foraging in open areas may also be favoured because of the greater ease of prey capture in the absence of obstructions, and it is also in such areas that sun patches form (discussed below). However this convenient linear feeding habitat is a man-made artefact. It is probably of benefit to the odonates and certainly convenient for the investigator, but the question remains; do these same factors apply also in natural gaps? Casual observation suggests that feeding territories are maintained in small gaps and at the margins of large gaps. Linear gaps not unlike the present study area do occur where a single large tree has fallen. However independent studies are needed to establish the extent of artificiality in this study.

It is clear that foraging activity is higher in sun patches than in shadow and foraging success is greater. However the causes of this are not certain. There is little evidence to suggest that prey density is higher in the sun, as found in temperate sun spots by Watanabe et al. (1987). It is unlikely that sun spots are preferred for thermoregulatory reasons, since, apart from the high ambient temperature (28–32°C in shade), preferred perches near sun patches were mostly at least partially shaded. Individuals exposed to direct sunlight by the shifting sunbeams usually relocated to a shaded perch after about 5 min of exposure.

One possible explanation for increased activity and success in sun patches is that prey flying in sunlight are more visible to the foraging *L. hyalina*. This explanation

Table 2. Numbers of insects less than 4 mm in length captured in Malaise traps in forest and along the track, orientated either north-south (perpendicular to the track) or east-west (parallel to the track).

	North-south	East-west	Total
Forest	224	286	510
Track	641	193	834
Total	865	479	1,344

is especially compelling given that in the forest under-storey the prey must be discerned against a variegated backdrop of vegetation, whereas the odonate eye is best adapted to perceiving prey against a backdrop of plain sky (Corbet 1999: 342). It is noteworthy also that foraging was maximal in mid afternoon during a period of high illumination but probably not maximal prey density, since swarms of small Diptera tend to become more frequent after 16:00 h, at which time foraging is drawing to a close. However after this time illumination of the under-storey up to 2 m is poor, although the slanting rays of the sun penetrate the subcanopy, where *L. hyalina* does not venture. Compared with other studies recorded capture rates were high, perhaps because the prey were mostly slow moving members of the aerial 'plankton'.

Enhanced prey visibility may have two effects on foraging behaviour. Firstly, prey illuminated by sunlight can probably be perceived from a greater distance, hence the effective foraging area of an individual is increased, an effect which would explain the higher foraging rates observed. Secondly, prey which are better illuminated may also be more at risk from a successful attack after detection. It was shown that foraging success was higher in sunlight. However it is unclear if this was because prey detected at the start of a foraging flight were captured more effectively or if sorties were undertaken before prey were sighted and prey were detected at a higher rate in the sunlight. Experimentally untangling these effects in such tiny insects would be challenging.

Previous work on feeding behaviour has identified occasional interspecific competition and aggression (Corbet 1999: 369). There were several other species present in the study area, some perching and defending feeding territories. The much larger *Agrionoptera sexlineata* occurred at low density, and *Brachygonia oculata*, a small libellulid somewhat larger than *L. hyalina*, was present at one-third to one-half the density of that species. In behaviour *B. oculata* was rather similar to *L. hyalina*, perching low beside the trail and forming numerous feeding territories involving immature males and females. Interspecific aggression was, however, seldom observed and it is likely that analysis would reveal subtle differences in preferred perch sites and prey range.

Corbet (1999: 361) lists and classifies strategies used by odonates to increase foraging efficiency. Several of these may be observed in *L. hyalina*, namely: 'A.2' Foraging at a persistent prey concentration caused by a gap in the forest and 'E', Defending a foraging site from exploitation by other predators. This is the first recorded example of 'E' in Zygoptera. I do not consider strategy 'A.1.5', foraging

at concentrations of prey at sun flecks in shaded surroundings, to apply in this case, as there is no evidence that the prey actually concentrate in sun patches. Rather, they probably pass through them on their progress along the track. Corbet (1999: 364) was referring to the work of Watanabe et al. (1987), who found sun-spots in temperate forest concentrated prey, or at least made them more active, due to increased ambient temperature. This effect does not occur in lowland equatorial forest. To these strategies can be added a possible new strategy which falls into category 'B', Increasing capture success by: [B.4] concentrating in situations where prey visibility is enhanced by overhead sunlight. Such enhancement would be particularly strong when the background is in deep shade, as is the norm in the tropical rain forest under-storey.

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REFERENCES

- Baird, J.M. & M.L. May, 1997. Foraging behaviour of *Pachydiplax longipennis* (Odonata: Libellulidae). *Journal of Insect Behavior* 10: 655-678.
- Corbet, P.S., 1999. Dragonflies: behaviour and ecology of Odonata. Harley Books, Colchester.
- Clark, P.J. & F.C. Evans, 1954. Distance to nearest neighbour as a measure of spatial relationships in population. *Ecology* 35: 445-453.
- Gorb, S.N., 1994. Female perching behaviour in *Sympetrum sanguineum* (Müller) at feeding places (Anisoptera: Libellulidae). *Odonatologica* 23: 341-353.
- Orr, A.G., 1996. Territorial and courtship displays in Bornean Chlorocyphidae (Zygoptera). *Odonatologica* 25: 119-141.
- Orr, A.G., 2001. An annotated checklist of the Odonata of Brunei with ecological notes and descriptions of hitherto unknown males and larvae. *International Journal of Odonatology* 4: 167-220.
- Orr, A.G., 2003. A guide to the dragonflies of Borneo, their identification and biology. Natural History Publications (Borneo), Kota Kinabalu.
- Orr, A.G. & P.S. Cranston, 1997. Hitchhiker or parasite? A ceratopogonid midge and its odonate host. *Journal of Natural History* 31: 1849-1858.
- Parr, M.J., 1983. An analysis of territoriality in libellulid dragonflies (Anisoptera: Libellulidae). *Odonatologica* 12: 39-57.
- Thompson, D.J., 2000. On the biology of the damselfly *Vestalis amabilis* Lieftinck in Borneo. *International Journal of Odonatology* 3: 179-190.
- Watanabe, M., N. Ohsawa & M. Taguchi, 1987. Territorial behaviour in *Platycnemis echigoana* Asahina at sunflecks in climax deciduous forests (Zygoptera: Platycnemididae). *Odonatologica* 16: 273-280.